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THE FIRST THRIPS SPECIES (INSECTA) INHABITING LEAF DOMATIA: *DOMATIATHRIPS CUNNINGHAMII* GEN. ET SP. NOV. (THYSANOPTERA: PHLAEOTHRIPIDAE)

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Abstract.—A new genus and species of tubuliferan Thysanoptera is described, *Domatiathrips cunninghamii,* which seems to be related to a group of moss-feeding species. With an adult body length of scarcely 1 mm, all life stages of the thrips were found living solitarily inside leaf domatia of a Rubiaceous under-story rain-forest tree in Costa Rica. The literature on the significance of leaf domatia and their relationships to arthropods is discussed.

Domatia have been defined as plant-produced chambers that house animals, differing from galls in that they are not induced by their inhabitants. In giving this definition, O'Dowd and Willson (1991) recognized two principal types: ant domatia, usually in hollow stems, thorns and petioles; and mite domatia, on the under-side of leaves in the axils of primary and secondary veins. The occurrence of other organisms in these plant structures seems to be regarded as largely casual.

The purpose of this paper is to record the presence of all life stages, egg to adult, of a minute phlaeothripine Thysanopteran insect within the leaf domatia of a rainforest understorey tree in Costa Rica. The presence of these insects, apparently obligatorily but with no obvious benefit to the plant, suggests a reconsideration of the views of Jacobs (1966), who questions the necessity for a single mutualistic explanation for leaf domatia.

The thrips species, which is described here as a new genus and species, is one of the smallest members of this insect order. It was first discovered by Saul Cunningham, of the University of Connecticut, within the leaf domatia of *Psychotria graciliflora* Bentham (Rubiaceae) at La Selva Research Station in Costa Rica. According to Dr. Orlando Vargas of La Selva, who kindly identified this tree, two similar species of *Psychotria* are known at this site, but only *graciliflora* has domatia on its leaves in contrast to *P. chagrensis* Stand.

THE DOMATIA

Psychotria graciliflora is an understorey tree, with a curious growth habit such that the branches with their small leaves tend to form flat layers rather like an African *Acacia* tree. It shares this habit with certain other rainforest understorey trees, such as *Randia karstenii* Polakowsky (Rubiaceae). However, judging from herbarium material at The Natural History Museum, the growth habit, leaf size and development of domatia are variable in *P. graciliflora,* possibly in relation to the degree of shading by top canopy trees. The leaves collected at La Selva were small, 20 to 40 mm, and many had small epiphytes on the surface.

Domatia were not observed on the youngest or smallest leaves, but varied in number from one to three on those leaves on which they were present. Each domatium is situated at the junction of a secondary vein with the midrib, and extends basally from its pore along the side of the midrib, between this and a rather thickened, basally curved, lateral vein (Fig. 5). In the absence of a domatium, a secondary vein is not curved basally but joins the midrib at an obtuse angle, and so the development of a domatium must be determined early in the ontogenesis of a leaf. The form of these domatia is that of a "pocket" (Jacobs, 1966), in that they are completely enclosed with one terminal opening. The inner cavity is about 1.5 mm long, and narrows gradually from an almost spherical chamber 0.4 mm in diameter under the pore to a rounded apex about 0.1 mm in diameter.

A sample of twigs bearing about 200 leaves was taken from each of three *P. graciliflora* trees at La Selva; two were close together under the canopy of old *Theobroma* cacao L., the third was 20 meters away within primary forest. The tree was common at this site, and ranged in size up to about two meters. The leaves in each sample were examined using transmitted light, because the domatia are translucent and their contents can thus be observed easily. Nothing was found in the domatia of the leaves from the third tree, but the thrips listed below were equally distributed between the leaves of the other two trees. No mites were observed in these domatia, but they could have been overlooked.

THE THRIPS

Phlaeothripine Thysanoptera species deposit their eggs, one at a time, on the surface of their feeding substrate using a chute-like ovipositor (Mound and Heming, 1991). They have two feeding larval stages, and three non-feeding pupal stages before the adults emerge. Examples of each of these immature stages were found in the leaf domatia studied. Like many other phlaeothripines, the adults of this species are either winged or wingless, although it is possible that winged males are not developed.

Thrips were found in less than 10% of the leaves collected, and their distribution was evidently clustered. On some twigs the leaves had no thrips, but on a few twigs most leaves bore one or more thrips. A few leaves had one thrips in each domatium (egg, larva, pupa or adult), but no domatium had more than one inhabitant. Only one thrips was found outside of a domatium; this was a winged adult female which was found walking on the sample when this was removed from the collecting bag several hours later. The author usually collects thrips by beating plants over a plastic tray, the adhesive tarsal pad of these insects causing them to stick to the plastic surface (Palmer, Mound and DuHeaume, 1989). No thrips were taken when these trees were beaten, suggesting that each insect was inside a domatium at the time.

The eggs were found singly, laying transversely at the bottom of the domatia. The other instars were usually found head down in a domatium, although when disturbed an adult would back-up into the main cavity and then try to emerge head first through the pore.

These observations all suggest that this thrips species was not casual within the domatia. Due to their enclosed situation they could not be observed actually feeding on the leaf tissue and, curiously, the species appears to be related to a group of species normally found in association with mosses and lichens (Mound, 1989). Moreover,

a green pigment was pressed out of the gut of several adult specimens when they were being prepared onto microscope slides. Such a pigment has only been observed before when preparing moss-feeding thrips, never with the much more common leaf-feeding species on dicotyledonous plants. Thus the possibility cannot be excluded that the thrips may be feeding on epiphytic micro-organisms on the leaf surface.

The only thrips species known to live in a comparable situation is *Rhopalothripoides froggatti* (Bagnall) which breeds within the cavities of the leaf nectaries of certain pinnate-leaved *Acacia* trees in Australia. In *Acacia paramattensis* Tind. up to 20 eggs have been observed in one of these leaf glands, although usually no more than two adults have been found (Mound, 1971). However, crawling into small spaces is an essential aspect of thrips biology (Mound, 1993), and further examples of such cryptic associations may yet be found.

DISCUSSION

The evidence for mutualism between ants and plants is extensive and convincing. Hölldobler and Wilson (1990) tabulate the wide range of such relationships, and Huxley and Cutler (1991) discuss many ant-plant interactions in considerable detail. In contrast, the evidence for mutualisms between mites and plants is largely based on circumstantial evidence. O'Dowd and Willson (1989) analyze a wide range of mite domatia, but their evidence for the suggestion that leaf domatia are produced by plants in order to house mites lacks an experimental base.

The taxonomic distribution of leaf domatia amongst the flowering plants is reviewed by O'Dowd and Willson (1989). These structures occur in most of the major lineages, apart from the monocotyledons and the Caryophyllales. They are particularly common amongst the Rubiales of the Asteridae, the most advanced lineage of dicotyledons. These authors also tabulate the remarkably large number of families of mites, not all identified but probably 27, that they collected from the leaves of 36 plant species with leaf domatia in the Australasian region. Many species in these mite families are known to be fungivorous or predatory, and the high frequency with which such mites were found on the leaves of these plants is taken as evidence in favour of mutualism between mites and plants—the mites being assumed to keep away microfungi and phytophagous mites. O'Dowd and Willson (1991) point out that such a relationship could be tested experimentally. However, Jacobs' experiments (1966) demonstrated that domatia developed normally on several trees in the absence of mites, and he maintains that views on mutualism owe as much to wishful thinking as to careful observation.

The difficulty is that leaves, particularly in the tropics, provide an extensive and heavily exploited habitat for microorganisms (Hawksworth, 1991) as well as small arthropods such as mites and thrips. Moreover, mites, like thrips (Mound, 1993), have the habit of crawling into small spaces. It is true that leaf domatia seem to be more frequent on tropical than on temperate plants, and also that leaf epiphytes are more common in the tropics. But these correlations cannot be taken to demonstrate mutualism in anything other than a very broad sense. Small arthropods can be expected to make use of any cavities slightly larger than their body size simply as shelters in which to reduce water loss through respiration. O'Dowd and Willson (1989) summarize the various other suggestions which have been made concerning

the biological significance of leaf domatia, but the advantages to the plants remain obscure and undemonstrated. Certainly, the provision of pockets in which minute thrips can breed seems unlikely to benefit the plants, and the suggestion of mutualism with other organisms remains unproven.

Domatiathrips, new genus

Minute macropterous or micropterous Phlaeothripinae-Williamsiellina. Antennae 8-segmented, III with 2 sense cones, IV with 3 sense cones, VIII not narrowed at base. Head longer than wide; stylets relatively broad, very widely separated with a maxillary bridge, retracted to postocular setae. Pronotal epimeral sutures complete or incomplete; praepectal plates present, mesopraesternum broad; meso and metathoracic furcae not fused in micropterae, metathoracic sterno-pleural sutures not developed in either morph. Fore tarsus with inner apex recurved into a small tooth in both sexes. Forewings parallel sided, with few duplicated cilia. Pelta D-shaped; macropterae with two pairs of wing retaining setae on tergites II–VII. Major setae capitate, including B1 on tergite IX. Sternites II–VII with median pair of marginal setae not longer than the discal setae. Male without a glandular area on sternite VIII; setae B2 on tergite IX short and pointed.

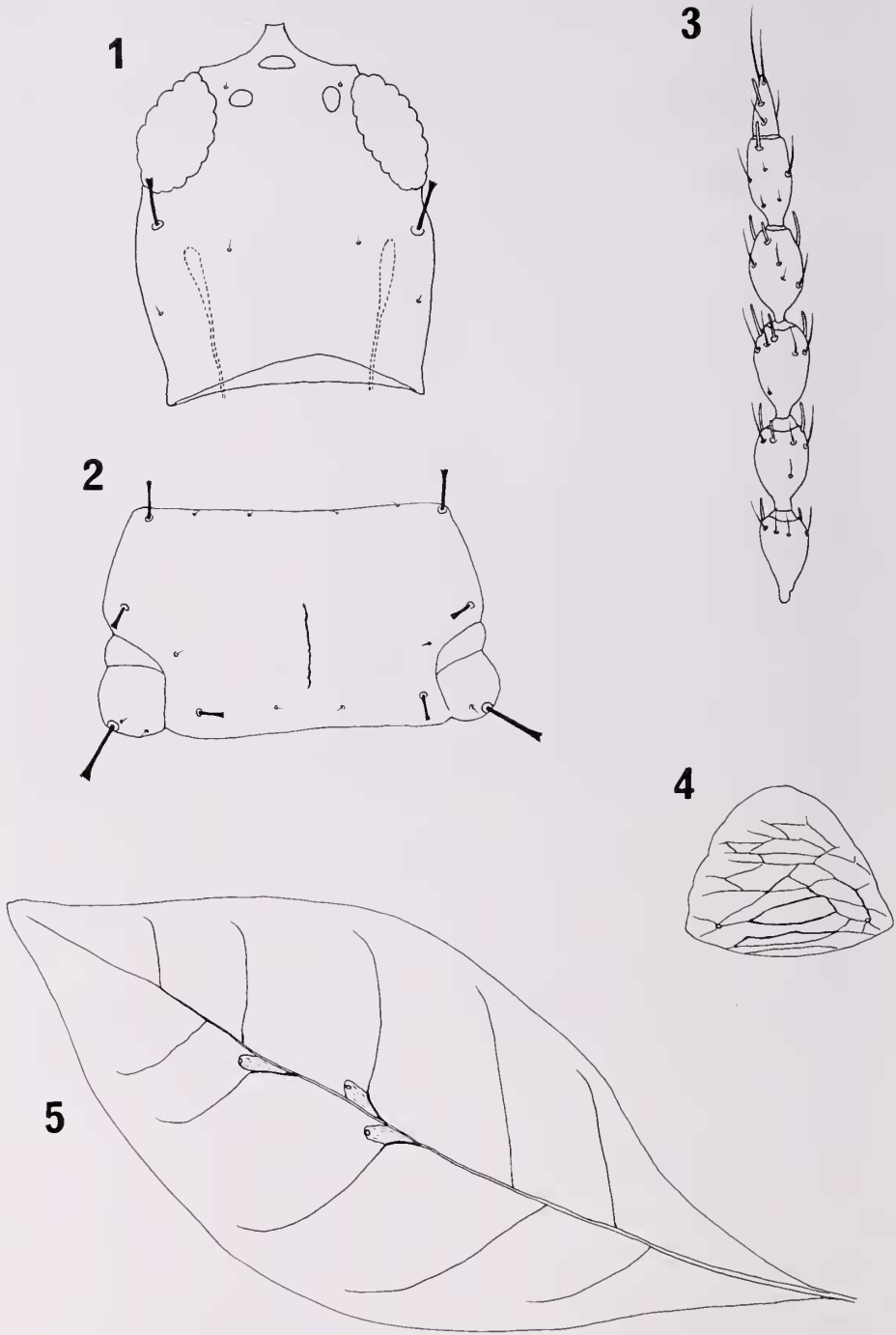
Type species *Domatiathrips cunninghamii.*

This new genus seems to be related to *Williamsiella* in the small size of the third antennal segment, and the relatively broad maxillary stylets. Unlike other members of the Williamsiellina the setae on tergite IX are shorter than the tube, and the median setae on the sternites are exceptionally short. The only species of *Williamsiella* with a similar long head is *longiceps* Hood, but that has seven-segmented antennae, the stylets restricted to the mouth cone, a transverse pelta, and a transverse glandular area on sternite VIII of the male.

Domatiathrips cunninghamii, new species

Female macroptera. Colour light brown; tarsi, apices of all femora, extreme base of tube, and antennal segments I–VI pale. Forewing pale with base and scale dark, and lightly shaded in basal half. Major setae dark.

Head (Fig. 1) with postocular setae wide apart; vertex without sculpture; mouth cone rounded. Antennae (Fig. 3) with segment V largest, 2 sense cones on III and 3 on IV–VI. Pronotum without sculpture, epimeral sutures almost complete, anteromarginal setae minute (Fig. 2). Mesonotal lateral setae minute; metanotum almost without sculpture, median setae small and acute. Fore tarsus with small hook on inner apical margin, much smaller than hamus. Forewing sub-basal setae reduced, 3 or 4 duplicated cilia present. Pelta D-shaped with distinct sculpture (Fig. 4); abdominal tergites with median area sculptured, wing retaining setae straight on tergite II but sigmoid on III–VII; the anterior pair of each wing retaining setae much smaller than the posterior pair on these tergites; tergite IX B1 setae short and capitate, B2 and B3 acute, shorter than tube; tube scarcely half as long as head, terminal setae shorter than tube. Sternites II–VII with 2 pairs of marginal setae and 3 pairs of discal setae; marginal setae on VIII much longer than on preceeding sternites. Measurements (Holotype ♀ macroptera in μm): Body length 1,200. Head, length 135; width 110; postocular setae 20. Pronotum, length 80; width 140; setal lengths—am 3, aa 15, ml



Figs. 1–5. 1–4. *Domatiathrips cunninghamii*—1, Head; 2, Pronotum; 3, Antennal segments III–VIII; 4, Pelta. 5, *Psychotria graciliflora* leaf, showing axillary domatia.

15, epim 25, pa 12. Metanotal median setae 12. Forewing, length 450; maximum width 40; sub-basal setae 5, 15, 15. Tergite IX setae—B1 30, B2 45, B3 50. Sternite VII marginal setae B1 10. Tube, length 75; terminal setae 60. Antennal segments length—I 18, II 33, III 28, IV 30, V 33, VI 33, VII 33, VIII 25.

Female microptera. Very similar to macroptera in colour and structure except—ocelli scarcely developed; forewing 40 μm long without setae, tergal wing retaining setae short and straight on II, posterior pair on III–VI also short.

Male microptera. Very similar to female except—smaller, with tergal wing retaining setae even more reduced, and a slightly larger fore tarsal tooth; tergite IX B2 setae short, sternite VIII without a glandular area; pseudovirga well developed and parallel sided. Measurements (paratype ♂ in μm): Body length 1,050. Head, length 130; width 100; postocular setae 25. Pronotum, length 85; width 135. Tergite IX setae—B1 30, B2 25, B3 50. Tube length 80.

Immature stages. Egg: About 400 μm long; surface of chorion with typical hexagonal plates; the apex of three slide-mounted eggs with a curious dome-shaped swelling which appears to break through the chorion. Larvae: Major setae capitate as in adult, tube with one pair of exceptionally long setae; first instar pale with red hypodermal pigment in pro- and metathorax; second instar with pronotum and tube brown; pupae pale with scattered red pigment spots.

Material studied. Holotype female macroptera: Costa Rica, La Selva Biological Research Station, Porto Viejo, Sarapiqui, on *Psychotria graciliflora* leaves, 27 April 1992 (L. A. Mound 2307), in BMNH. Paratypes: 6 female micropterae, 6 male micropterae, removed from leaf domatia of the same sample of *Psychotria graciliflora* from which the holotype was collected.

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